# A new Eocene lineage of reticulate *Nummulites* (Foraminifera) from Kilwa district, Tanzania; a place for *Nummulites ptukhiani*?

Laura J. Cotton[a]*, Paul N. Pearson[b] and Willem Renema[a]

*[a]Naturalis Biodiversity Center, Darwinweg 2, 2333CR Leiden, The Netherlands; [b]School of Earth and Ocean Sciences, Cardiff University, Main Building, Park Place, Cardiff, CF10 3AT, UK*

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*Corresponding author. Email: laura.cotton@naturalis.nl

Reticulate *Nummulites* are a widespread and distinctive group of *Nummulites*, frequently used in biostratigraphy, but their evolution is poorly understood. Studies from the Western Tethys suggest they form a single lineage, the *Nummulites fabianii* lineage, with an increasing proloculus size over time. This has led to their use as one of the diagnostic taxa for larger benthic foraminiferal biostratigraphy. However, outside of this region additional taxa have been recorded. The most widely discussed example is *Nummulites ptukhiani,* which was described from Armenia, whose morphology does not fit with the *N. fabianii* lineage. This raises the question whether reticulate *Nummulites* are monophyletic, or the result of multiple independent convergent evolutionary

lineages. Here we present data from three newly identified populations of Lutetian to Bartonian reticulate *Nummulites* from the stratigraphically well-constrained Tanzania Drilling Project records, which shed new light on the ancestry of these aberrant forms. These populations are characterized by extremely large proloculi and unusual morphology. We demonstrate that the populations are consistent with an evolutionary lineage that is morphologically distinct but contemporaneous with the *N. fabianii* lineage of the Tethys. These forms are remarkably similar in external and internal morphology to the Armenian *Nummulites ptukhiani.* We therefore refer to them as the *N. ptukhiani* lineage. The existence of a second lineage of reticulate *Nummulites* indicates that their evolution is more complex than previously thought and raises questions as to whether they evolved from a common ancestor, or independently. It also underlines the importance of carrying out thorough studies of larger benthic foraminifera with independent stratigraphical control from outside of the Tethyan region to more fully understand their evolution and to enable accurate biostratigraphy.

**Keywords**: foraminifera; Eocene; biostratigraphy; evolution; *Nummulites*

## Introduction

The larger benthic foraminiferal genus *Nummulites* is found abundantly within shallow marine deposits of the Paleogene and is frequently used in biostratigraphical studies. However, the evolution of this genus is poorly understood. Reticulate *Nummulites* are a distinctive group within the *Nummulites*, easily distinguishable by their mesh-like external ornamentation. This external pattern is the manifestation of a more complex internal structure; whilst the majority of

*Nummulites* have simple open chambers, the chambers of reticulate *Nummulites* are partitioned. Traditionally, this group has been considered as a single lineage from *N. praebullatus* in the uppermost Ypresian–lowermost Lutetian to *N. fichteli* in the Chattian, and is referred to as the *N. fabianii* lineage (Schaub 1981; Papazzoni 1993; Less & Ozcan 2012). Successive species show a relatively consistent and well-documented trend of increasing proloculus size over time, although some minor variation between geographical populations occurs (Blondeau 1972; Schaub 1981; Papazzoni 1998; Özcan *et al.* 2009; Less & Özcan 2012). This has enabled them to be used as one of the diagnostic taxa in the Shallow Benthic Zones of Serra Kiel *et al.* (1998) – the biostratigraphical scheme for larger benthic foraminifera. However, this can be problematic, as the majority of studies of the reticulate *Nummulites* were based on material from the Western Tethys and whilst the *N. fabianii* lineage is relatively well established there (Blondeau 1972; Schaub 1981; Papazzoni 1993; Papazzoni 1998; Less & Ozcan 2012), studies from outside of that region have shown that not all forms fit with the characters and trends of this lineage (e.g. Bombita 1984; Papazzoni 1998; Sengupta 2000; Cotton & Pearson 2011; Sengupta *et al*. 2011). *Nummulites ptukhiani* Kacharava, 1969 was described from Armenia and was originally regarded as the ancestor of *N. fabianii* (Ptukhyan 1964; Schaub 1981). However, it is morphologically distinct from both Western Tethyan forms of the same age and from other members of the *N. fabianii* lineage (Karachava 1969; Blondeau 1972; Bombita 1981; Papazzoni 1998). Although the name *N. ptukhiani* is often used in literature to refer to non-Armenian type reticulates of this age (e.g. Schaub 1981), true *N. ptukhiani* should only refer to those individuals with the morphology described by Karachava (1969) which have a much larger proloculus than contemporaneous members of the *N. fabianii* lineage, along with thicker spiral laminae, a constant whorl height, a large central plug, joining of granules around the periphery and a comparatively angular axial

section (Karachava 1969). Additionally, several reticulate *Nummulites* from the Oligocene of India have unclear affinities, including an unusual saddle shaped form (Sengupta 2000; Sengupta *et al.* 2011) and in Tanzania, Priabonian and Rupelian forms show small but consistent differences to the Western Tethyan *N. fabianii* and *N. fichteli* (Cotton & Pearson 2011). The evolution of reticulate *Nummulites* therefore appears more complex than previously thought.

In this paper we present data from three newly discovered populations of Lutetian to Bartonian reticulate *Nummulites* that show unusual morphology from stratigraphically well-constrained Tanzania Drilling Project (TDP) records. These specimens raise further questions about complexities of reticulate *Nummulite*s evolution and their use as a biostratigraphical tool.

## Geological setting

Marine sediments of Aptian to Oligocene age crop out along a broad coastal belt in Tanzania south of the Rufiji River (Nicholas *et al.* 2006). These sediments are formally defined as the Kilwa group and are split into four formations: the Nangurukuru, Kivinje, Masoko and Pande formations (Nicholas *et al.* 2006). The Masoko Formation spans the middle Eocene with no apparent unconformities. Three TDP sites, TDP 18, 4 and 2 recovered material from Lutetian to Bartonian age that contain populations of reticulate *Nummulites*. The three sites are located in the south-east region of Tanzania within the Kilwa and Lindi districts (Fig. 1; TDP 2 – UTM 37L 555371 9013813; TDP 18 – UTM 37L 558640 8975370; TDP 4 – UTM 37L 578530 8900033 (Pearson *et al.* 2004; Nicholas *et al.* 2006)). The sediments and smaller benthic foraminiferal assemblages suggest the depositional environment for the Masoko Formation was bathyal outer shelf to continental slope, with water depths of over 300 m (Nicholas *et al.* 2006). The sediments are

primarily dark greenish grey clays with occasional massive, hard, sparry limestone beds rich in larger benthic foraminifera. The larger benthic foraminifera are also present in lower numbers within the clays, particularly close to the limestone horizons. Despite the quantity of transported material (both larger and smaller benthic foraminifera from the shelf) no reworked foraminifera from older formations have been found (Nicholas *et al.* 2006). The cores were dated using planktonic foraminiferal and nanno-fossil stratigraphy; TDP 2 is Lutetian in age, ranging from planktonic foraminifer Zone E7b and nannofossil zone NP14b/15a (undifferentiated) at the base to planktonic foraminifer Zone E9 and nannofossil zone NP15c at the top – the samples used in this study are from the upper part of this record, within planktonic foraminifera zone E9, TDP 18 is within the early Bartonian (E12/NP16-17) and TDP 4 is early to middle Bartonian (E13/NP17) (Pearson *et al.* 2004; Nicholas *et al.* 2006).

## Methods

Reticulate *Nummulites* specimens were picked from clay residues that had previously been prepared by washing through a 63 μm sieve for the studies of Pearson *et al*. (2004) and Nicholas *et al*. (2006). Samples containing populations used in this study are listed in Table 1. The sample names are in TDP format of site number/core number/meter within the core and the level within that meter is given in centimeters. All specimens were A forms and no B forms were found. Specimens from sites TDP 2 and 4 were relatively well preserved with little infill. These specimens were therefore examined using micro-computed tomography (micro-CT). A skyscan 1172 micro-CT scanner was used to scan the specimens. The scans were then reconstructed using the program n-recon and measurements taken from virtual thin sections using Dataviewer. Three-dimensional

segmentations of chamber lumen were created using Avizo software. Specimens from TDP 18 were infilled with calcite and therefore it was not possible to produce clear images of the internal structures using micro-CT. These specimens were prepared as oriented thin sections. Standard measurements of proloculus size, whorl radii, diameter and thickness were taken (see Fig. 2) and the number of chambers per whorl counted following the methods of Schaub (1981), Renema *et al.* (2003) and Papazzoni (1998). Two measurements of proloculus size, P1 and P2 (see Fig. 2), are included to enable comparison with the work of different authors.

## Systematic palaeontology

Order **Foraminiferida**

Suborder **Rotaliina** Delage & Herouard, 1896

Superfamily **Nummulitacea** de Blainville, 1827

Family **Nummulitidae** de Blainville, 1827

Genus ***Nummulites*** Lamarck, 1801

***Nummulites ptukhiani*** Kacharava, 1969

(Figs 5–7)

1964 *Nummulites praefabianii* Ptukhyan: 52, pl. 1, figs 5–8.

1969 *Nummulites ptukhiani* Kacharava: 497.

1984 *Nummulites ptukhiani* (Kacharava); Bombita: table 1, column 1; pl. 1, figs 1–7.

**Material.** A total of 19 individuals were studied from TDP 2, 24 individuals from TDP 18, and 11 from TDP 4. Specimens from multiple levels were combined in TDP 2 and 4, as they were closely spaced (see Table 1 for TDP levels). All specimens have been deposited in the collections of the Naturalis Biodiversity Center, numbers RGM 791865–791919.

**Description.** All specimens are A forms. Tests are inflated lenticular, with diameter up to 3230 μm, thickness up to 1740 μm; and a mean D/T ratio of 2.08 in specimens from TDP 2, 2.00 in specimens from TDP 18 and 1.75 in specimens from TDP 4. Spirally placed granules are placed on septal filaments and reticulation is visible. Granules are often more pronounced in the central region. In equatorial section the spire is regular and relatively constant in height, with a maximum of three complete whorls (Fig. 3). The spiral laminae are thick; up to half of the height of the chambers in the inner whorls. Chambers are generally taller than long in the inner whorl, particularly apparent within samples from TDP 2, and become wider than tall in outer whorls. Range values of chambers per whorl are given in Table 2. Septa are curved. In axial section the alar prolongation is partitioned, with the partitioning occurring to a greater degree within populations from TDP 18 and TDP 4 compared with those from TDP 2. Pillars are clearly visible, creating the surface granules and are particularly prominent in the umbilical region. A large central plug is visible in some specimens (particularly those from TDP 4). The largest morphological variation between populations is the proloculus size; specimens from TDP 2 have a P1 value of 204–329 μm with a single larger specimen measuring 563 μm (P2: 275–458 μm, single specimen: 665 μm), specimens from TDP 18 have a P1 value of 284–443 μm (P2: 376–584 μm) and from TDP 4 a P1 value of 464– 660 μm (P2: 507–735 μm), showing a successive increase with time (Fig. 4; complete measurements for all individuals are given in the supplemental online table).

To examine the chamber structure in more detail three-dimensional models of chamber lumen were constructed for a specimen from the oldest (TDP 2) and from the youngest samples (TDP 4; Fig. 7). The specimen from TDP 2 showed un-partitioned chambers in whorl 1 and very slight narrowing/partitioning within the alar prolongation in the late second and third whorls, however the alar prolongation remains largely open (Fig. 7A). The open alar prolongation indicate this form is not truly reticulate. The specimen from TDP 4 showed significant (near total) closure of the alar prolongation between the equatorial chamber lumen and the alar prolongation, and less severe additional partitioning within the alar prolongation (Fig. 7B). The chambers are relatively even in size and evenly distributed. A central region free from chambers can be seen in both specimens, indicating a central plug.

**Remarks.** The three populations show similar morphological characters; the gradient of the whorl plots, number of chambers per whorl and D/T ratios along with more qualitative traits suggest they are closely related. Though the proloculus measurements differ between the populations, all three are exceptionally large for middle Eocene reticulate *Nummulites* and show a steady increase over time (Fig. 4). In three-dimensional reconstruction specimens from TDP 2 show only very minor partitioning of the alar prolongation. However, specimens from TDP 18 and TDP 4 in axial section and the three-dimensional reconstruction of the specimen from TDP 4 show very clear partitioning of the alar prolongation and are therefore undoubtedly reticulate *Nummulites* species. Given the similarities in morphology between the populations and the trend seen within the proloculi we suggest that although the population from TDP 2 is not a true reticulate form it is related to the *Nummulites* of TDP 18 and TDP 4, and is an early form which has not yet developed full reticulations. The three populations therefore form an evolutionary lineage, with increasing

proloculus size and complexity of reticulations. However, they show distinct differences to the *N. fabianii* lineage from the Western Tethys.

The Tethyan series of reticulate *Nummulites* is generally considered as *N. praebullatus* Schaub, *N. bullatus* Azzaroli, *N. garganicus* Tellini, *N. hormoensis* Nuttall & Brighton (*N. "ptukhiani"* in Papazzoni 1998), *N. fabianii* Prever, *N. fabianii retiatus* Roveda and *N. fichteli* Michelotti (Schaub 1981; Papazzoni 1993; Papazzoni 1998; Less & Ozcan 2012). *Nummulites praebullatus* is the earliest known form, occurring in the upper Ypresian/lower Lutetian of Libya and has granules but not true reticulations. *Nummulites bullatus*, *N. garganicus* and *N. hormoensis* then successively span the Bartonian (Schaub 1981; Papazzoni 1998; Ozcan *et al.* 2009; Less & Ozcan 2012). These four species are contemporaneous to the Tanzanian forms described here and show the same transition from granulose, non-reticulate forms to reticulate forms. The external ornamentation of specimens TDP 2 and TDP 18 appears similar to that of *N. praebullatus* and *N. bullatus* as illustrated in Schaub (1981). However, the central plug is clearly visible in specimens from TDP 4, which likely developed from the large central pustules seen in the earlier forms, but does not occur in *N. hormoensis*. The D/T values when compared with those of Schaub (1981) and Papazzoni (1998) are similar, with the thickness being approximately half the diameter. Specimens of *N. hormoensis* in Papazzoni (1998) had a D/T ratio of approximately 1.9 – 2.25, which increases to 2.3 – 3.3 in *N. fabianii*. However diameter and thickness are thought to be influenced by environmental factors such as light levels, substrate and energy (Hallock & Glenn 1986; Racey 1992; Trevisani & Papazzoni 1996; Beavington-Penney & Racey 2004).

The internal morphology of the Tanzanian forms shows clear differences to that of the *N. fabianii* lineage. The proloculi of the Tanzanian specimens are much larger than those of their Tethyan counterparts; *N. praebullatus* is described as having a proloculus diameter (P1) of 90–100

μm, increasing to 150–220 μm in *N. hormoensis* in the Bartonian (Schaub 1981; Papazzoni 1998). The youngest member of this lineage, *N. fichteli* is described as having a proloculus diameter of 250–300 μm in Schaub (1981). Whilst the Tanzanian forms have proloculi sizes of up to 329 μm in the Lutetian, 443 μm in the lower Bartonian and up to 660 μm in the middle Bartonian. The earliest forms from Tanzania therefore have proloculi diameters comparable with some of the youngest forms of the Tethys and up to three times the size of their contemporaries. The whorls also show variation, with specimens from Tanzania showing a relatively constant spire height, contrasting with the spire of the *N. fabianii* lineage that tends to show a steady increase in height. The three populations from the Lutetian to Bartonian of Tanzania are therefore consistent with being from a separate lineage of reticulate *Nummulites* occurring in parallel with the *N. fabianii* lineage in the Western Tethys.

*Nummulites ptukhiani* has been recognized as not being part of the *N. fabianii* lineage (Kacharava 1969; see discussion in Papazzoni 1998). *Nummulites ptukhiani* is described as having a biconical test with a pronounced central knob, a large protoconch, up to 450 μm in the description of Kacharava (1969) and up to 600 μm in diameter in Bombita (1984), a constant spire and thick spiral lamella. Kacharava (1969) also describes the surfaces as showing spirally placed granules which are connected in the periphery which may indicate a similar internal structure to that seen in the three-dimensional reconstruction of the specimen TDP 18, where the peripheral part of the chamber lumen is separated from the alar prolongation. Whorl diagrams were also plotted from images of two specimens of *N. ptukhiani* provided by E. Zakrevskaya (Vernadsky State Geological Museum) and though slightly steeper than the average values from the Tanzanian populations, they were well within the spread of values from individuals (Fig. 3). This description is remarkably similar in both internal and external morphology to the forms we describe from Tanzania,

particularly the specimens from TDP 4 (see summary in Table 3). We assign the Tanzanian specimens to *N. ptukhiani* and refer to them as the *N. ptukhiani* lineage. Although the morphological variation between each of the three populations is as large as between named species in the *N. fabianii* lineage, at present the material is only known from three stratigraphical levels. We therefore refrain from separating the lineages into multiple species or subspecies until we better understand the heterogenic rates of morphological evolution within the lineage and natural divisions are more apparent.

## Discussion

Our results indicate that the evolution of reticulate *Nummulites* is more complex than previously thought. Whilst the presence of parallel reticulate *Nummulites* lineages is an important new discovery for understanding their evolution and biogeography, it also raises new questions about their origins. The earliest members of both lineages occur in the Lutetian, although *N. praebullatus*, the ancestor of *N. fabianii*, occurs slightly earlier than the earliest known Tanzanian form (Schaub 1981). *Nummulites praebullatus* is reported from Libya, which was part of the Tethys during the Eocene. Therefore whilst geographically part of the same continent, they were living within different oceanic provinces. Endemic forms of *Nummulites* showing advanced characters, including exceptionally large proloculi, are known to occur, e.g. *N. luterbacheri* from the early Eocene of Egypt (Wielandt 1999). Within the Nummulitidae, specimens of the genus *Cycloclypeus* from Fiji, again a single locality, also show exceptionally large proloculi compared to contemporary populations (Renema 2015). These cases appear similar to the Tanzanian *Nummulites*, with the exception that the later forms of *N. ptukhiani* apparently migrated at least to

the Armenian part of the Tethys where they co-occur with the *N. fabianii* lineage. Therefore although they may have had endemic beginnings they are certainly more widespread by the mid-late Bartonian.

Given the distinctive nature of the reticulate *Nummulites* as a group it is possible that the two lineages share a common ancestor in the early Eocene and the group consists of multiple branches, but no such form has yet been found. Alternatively, a polyphyletic origin is also possible. Convergent evolution is well known within the Nummulitidae, for example the evolutionary series *Heterostegina – Tansinhokella – Spiroclypeus* has been shown to evolve twice within the Indo-Pacific – within the Eocene and again within the Oligo–Miocene (Lunt & Renema 2014). Whilst in this case the two lineages are easily identified as having evolved convergently due to their separation in time, this is more complicated when the lineages are occurring within the same time frame and regions. In either case, the co-occurrence of multiple lineages of reticulate *Nummulites* underlines the importance of not relying on a single geographical realm as a standard biostratigraphical correlation and of independent dating of species ranges. Many of the major works on *Nummulites* and subsequent studies are largely Tethyan-based. Whilst this provides a good basis for further work, equally thorough studies are needed in other regions to enable a fuller and clearer understanding of *Nummulites* evolution and enable accurate use for biostratigraphy.

## Conclusions

The three new morphotypes described here form an evolutionary series and show clear differences to their contemporaneous Tethyan counterparts, therefore indicating they are separate from the well-known *Nummulites fabianii* lineage. We assign these populations to the species *Nummulites*

*ptukhiani* Kacharava, 1969 and refer to them as the *N. ptukhiani* lineage. This lineage also includes the formerly unexplained *N. ptukhiani* described from Armenia, indicating it is not an endemic species. Though it remains uncertain as to whether the *N. fabianii* and *N. ptukhiani* lineages share a common ancestor or evolved convergently the existence of a second contemporaneous lineage of reticulate *Nummulites* indicates the evolution of this group is more complex than previously thought. This finding has important implications for the use of the current biostratigraphy and whether it can be reliably be applied outside of the Tethyan region. Further studies of reticulate *Nummulites* populations on a global scale need to be carried out to better understand the evolutionary mechanisms and distributions of this distinctive and important group.

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## Supplemental material

Supplemental material for this article can be accessed at:

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## Table captions

**Table 1.** Sample list of specimens. Sample numbers are in the TDP format: site number/core number/core section depth (cm), cc indicates sample from the core catcher at the base of the core. Planktonic foraminiferal zones are those of Wade *et al*. 2011.

**Table 2.** Range values of chambers per whorl from TDP 2, TDP 18 and TDP 4 populations to the nearest whole chamber, with number of specimens in brackets.

**Table 3.** Summary of characters of *Nummulites ptukhiani* from the original description of Kacharava (1969) and populations described in this paper, for comparison.

## Figure captions

**Figure 1.** Location map showing the position of sites TDP 2, TDP 18 and TDP 4.

**Figure 2.** Schematic drawing of a specimen of *Nummulites* showing measurements taken. Chamber counts are shown for the first whorl. Abbreviations: P1, vertical proloculus height; P2, horizontal proloculus height; WD, distance from centre of proloculus to edge of deuteroloculus; W1, W2, W3, successive whorl radii.

**Figure 3.** Whorl diagrams for reticulate *Nummulites* populations for **A,** TDP 4; **B,** TDP 18; **C,** TDP 2 . Mean values shown as a single line, shaded area represents spread of values from

individuals. **D,** mean plots of the three TDP populations shown with mean plot of two *N. ptukhiani* individuals measured from images of specimens provided by E. Zakrevskaya (Vernadsky State Geological Museum, Moscow).

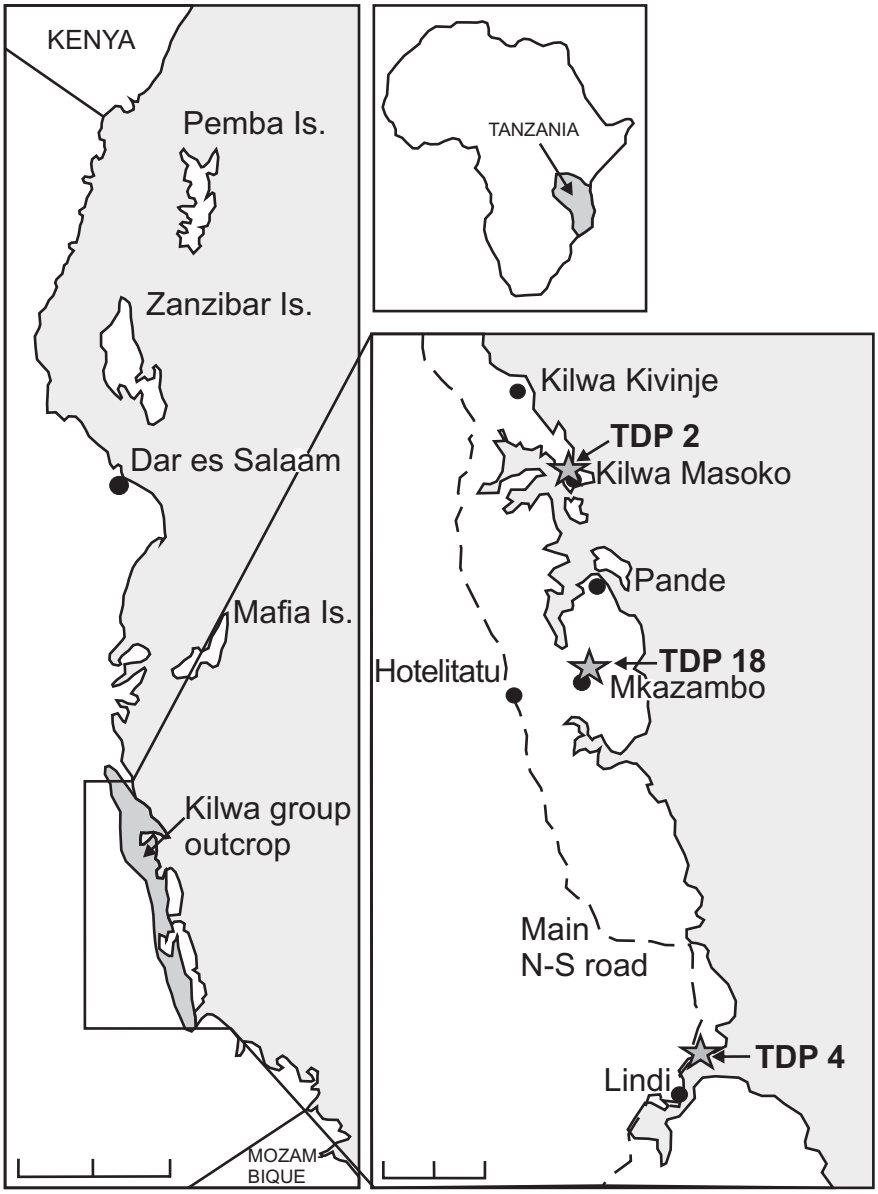
**Figure 4.** Diagram showing stratigraphical positions of TDP 2, TDP 18 and TDP 4 alongside histograms showing distribution of proloculei sizes of respective reticulate *Nummulites* populations; pale grey bars show P1 values and dark grey bars show P2 values.

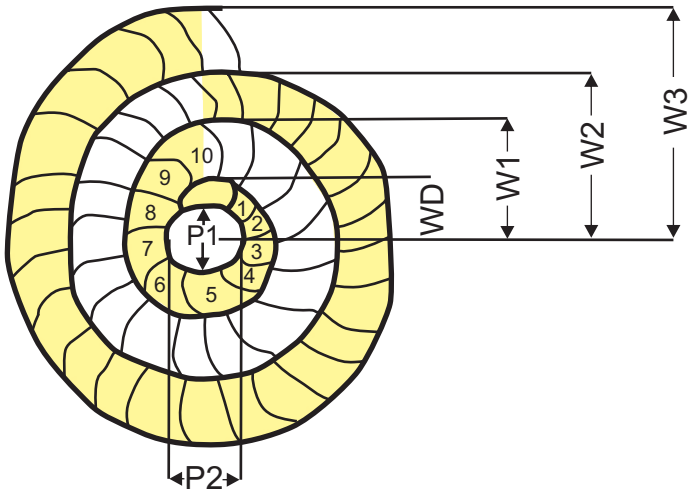
**Figure 5.** *Nummulites ptukhiani*, virtual sections from micro-CT scans: **A–E, G,** population from TDP 2 (Lutetian); **A,** equatorial section, specimen TDP 2/16 b; **B,** equatorial section, specimen TDP 2/16 h; **C,** equatorial section, specimen TDP 2/16 c; **D,** axial section, specimen TDP 2/16 h; **E,** external surface, specimen TDP 2/16 g; **G,** axial section, specimen TDP 2/16 b. **F, H–K,** population from TDP 4 (middle Bartonian); F, axial section, specimen TDP 4/5/5 5-10 cm f; H, axial section, specimen TDP 4/5/5 44–50 cm 1; I, equatorial section, specimen TDP 4/5/5 5–10 cm f; J, equatorial section, specimen TDP 4/5/5 5–10 cm c; K, equatorial section, specimen TDP 4/5/5 44–50 cm 1. Scale bar 500 μm.

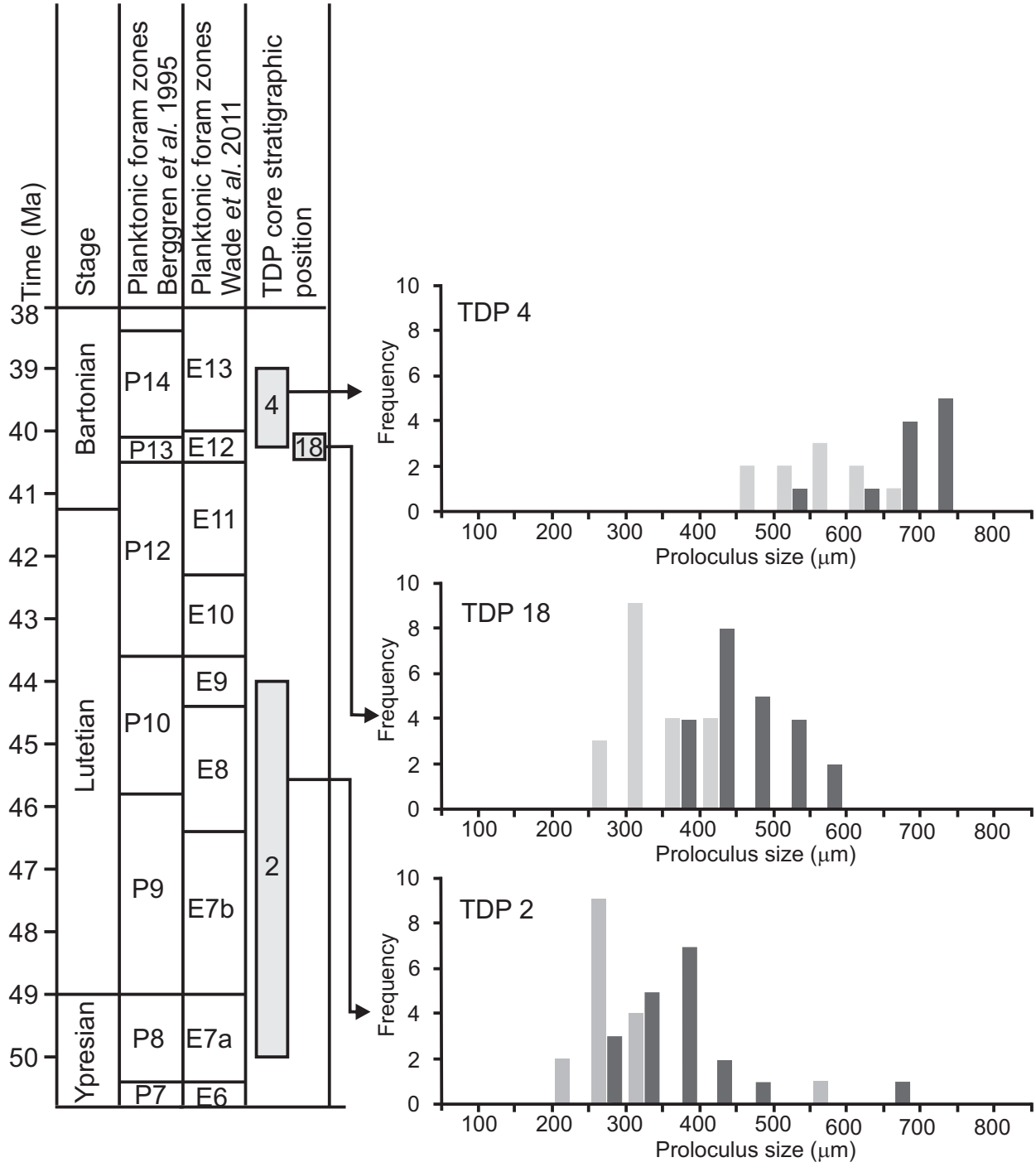
**Figure 6.** *Nummulites ptukhiani*, photomicrographs from oriented thin sections: **A, B,** population from TDP 4 (middle Bartonian); **A,** external surface, specimen TDP 4/5/5 5–10 cm a; **B,** external surface, specimen TDP 4/5/5 5–10 cm c. **C–H,** population from TDP 18 (lower Bartonian); **C,** external surface, specimen TDP 18/16/2 0–8 cm c; **D,** equatorial section, specimen TDP 18/16/2 0–8 cm 24; **E,** equatorial section, specimen TDP 18/16/2 0–8 cm 1; **F,** equatorial section, specimen

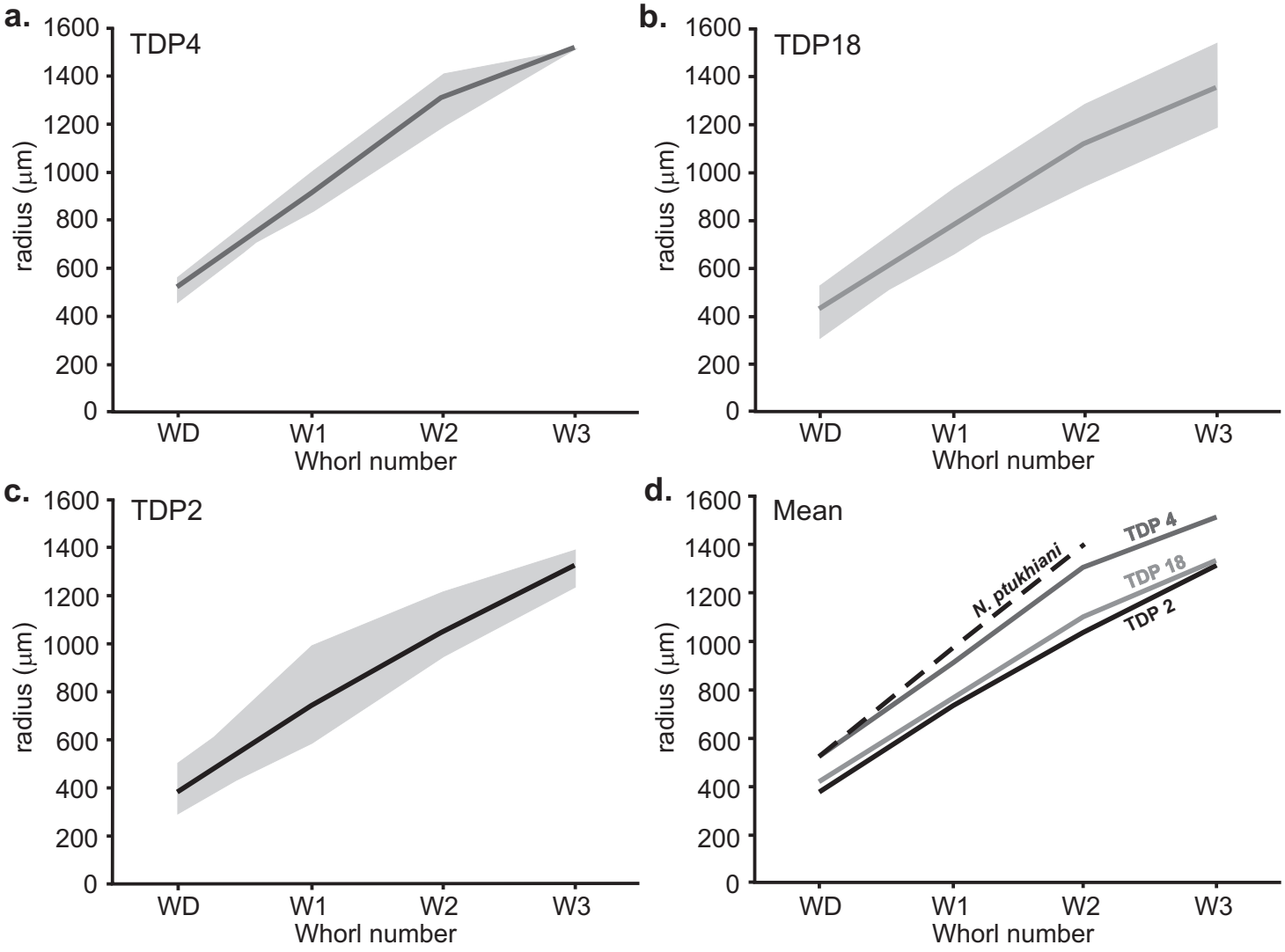
TDP 18/16/2 0–8 cm 29; **G,** axial section, specimen TDP 18/16/2 0–8 cm 41; **H,** axial section, specimen TDP 18/16/2 0–8 cm 40. Scale bar 500 μm.

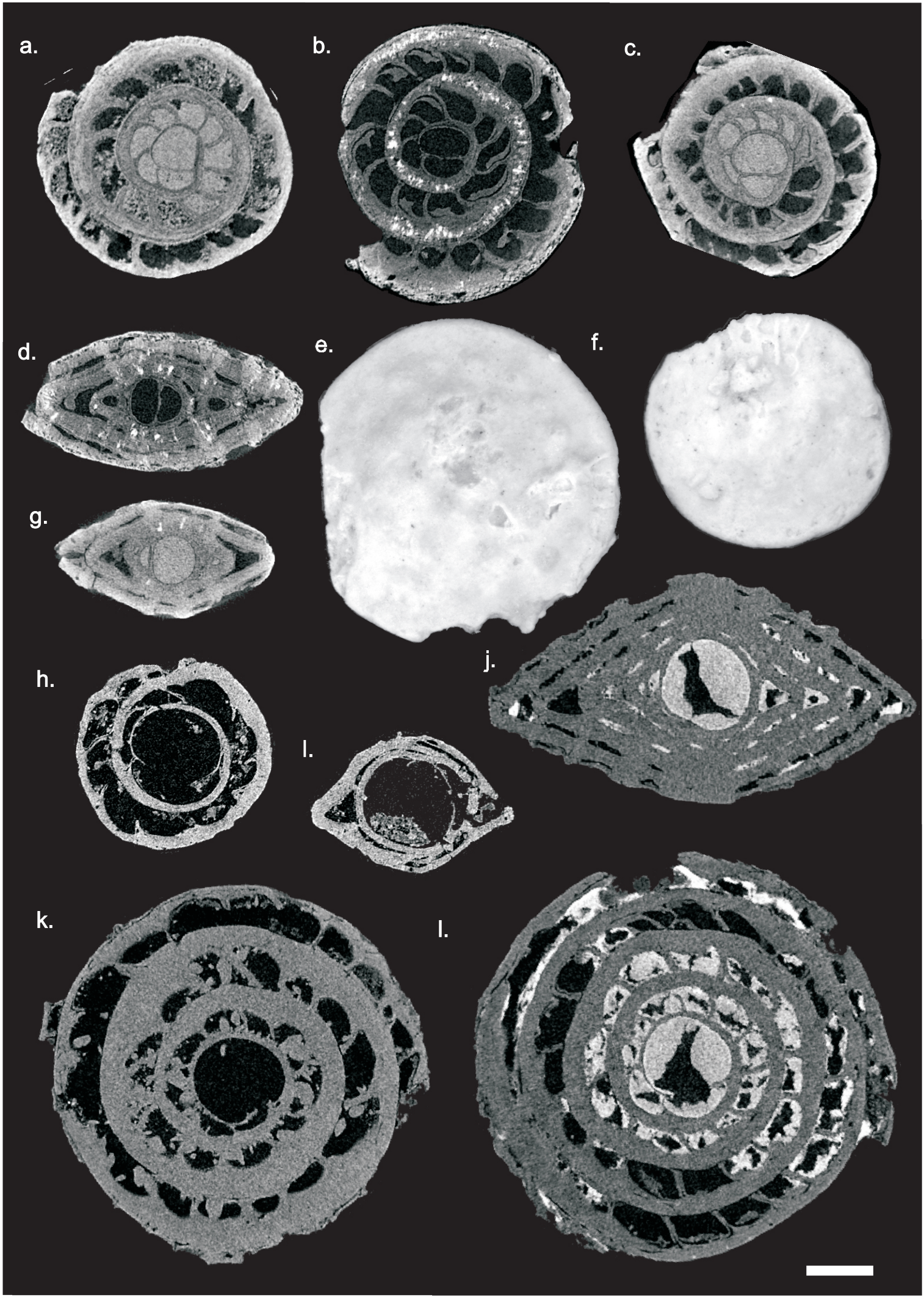
**Figure 7.** Three-dimensional rendering of chamber lumen from specimen **A–C,** TDP 2/16 b (Lutetian) and **D–G,** TDP 4/5/5 5–10 cm b (middle Bartonian) showing **A, D,** proloculi; **B, E,** whorl 1; **C, F,** whorl 2; and **G,** whorl 3 of respective specimens. Slight narrowing of alar prolongation is visible in the alar prolongation of the specimen from TDP 2 compared with almost full partitioning in that of the TDP 4 specimen. Scale bar 1 mm.

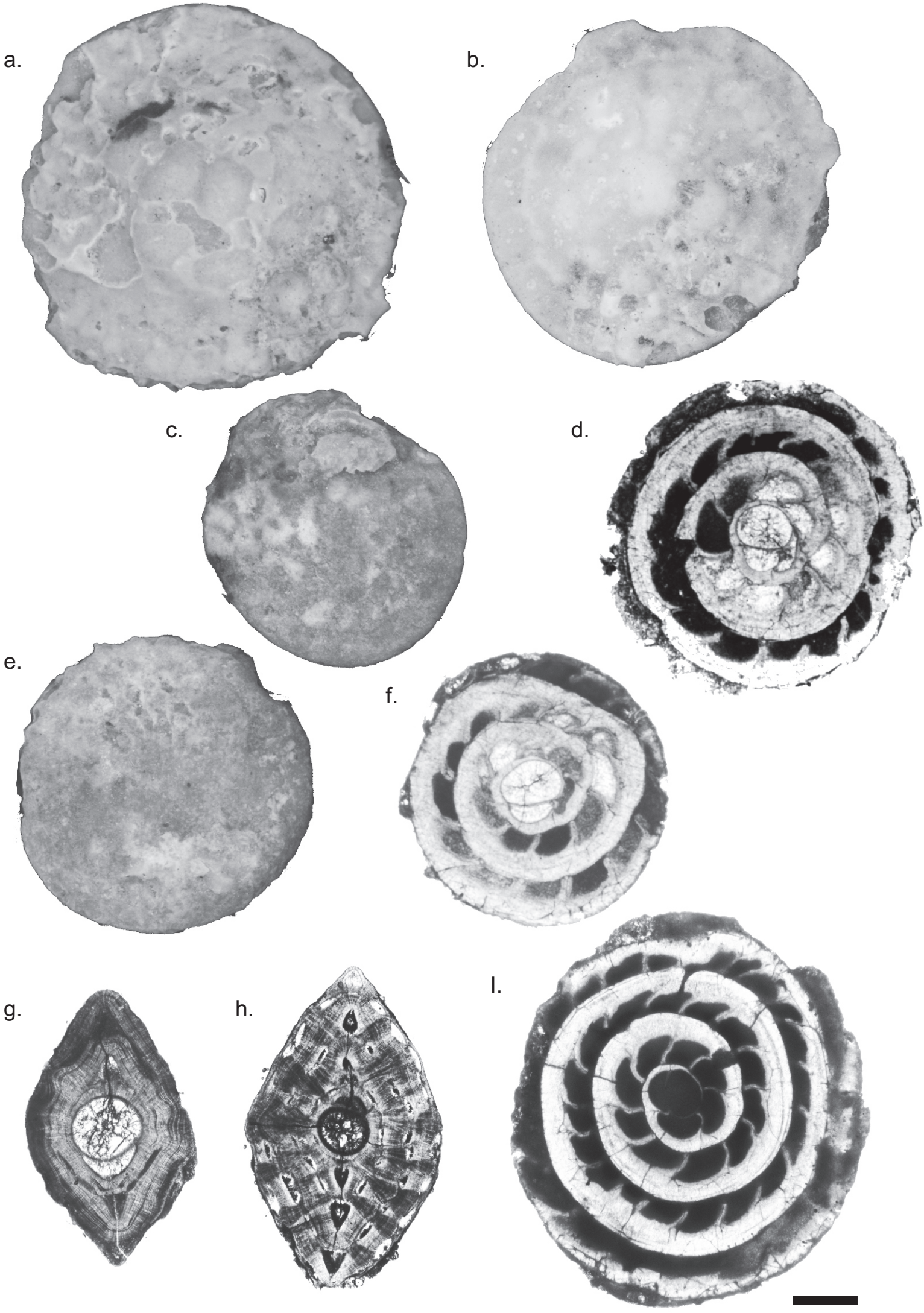

KENYA
Pemba Is.
Zanzibar Is.
Dar es Salaam
Mafia Is.
Kilwa group
outcrop
MOZAM
BIQUE
TANZANIA
Kilwa Kivinje
TDP 2
Kilwa Masoko
Pande
Hotelitatu
TDP 18
Mkazambo
Main
N-S road
TDP 4
Lindi

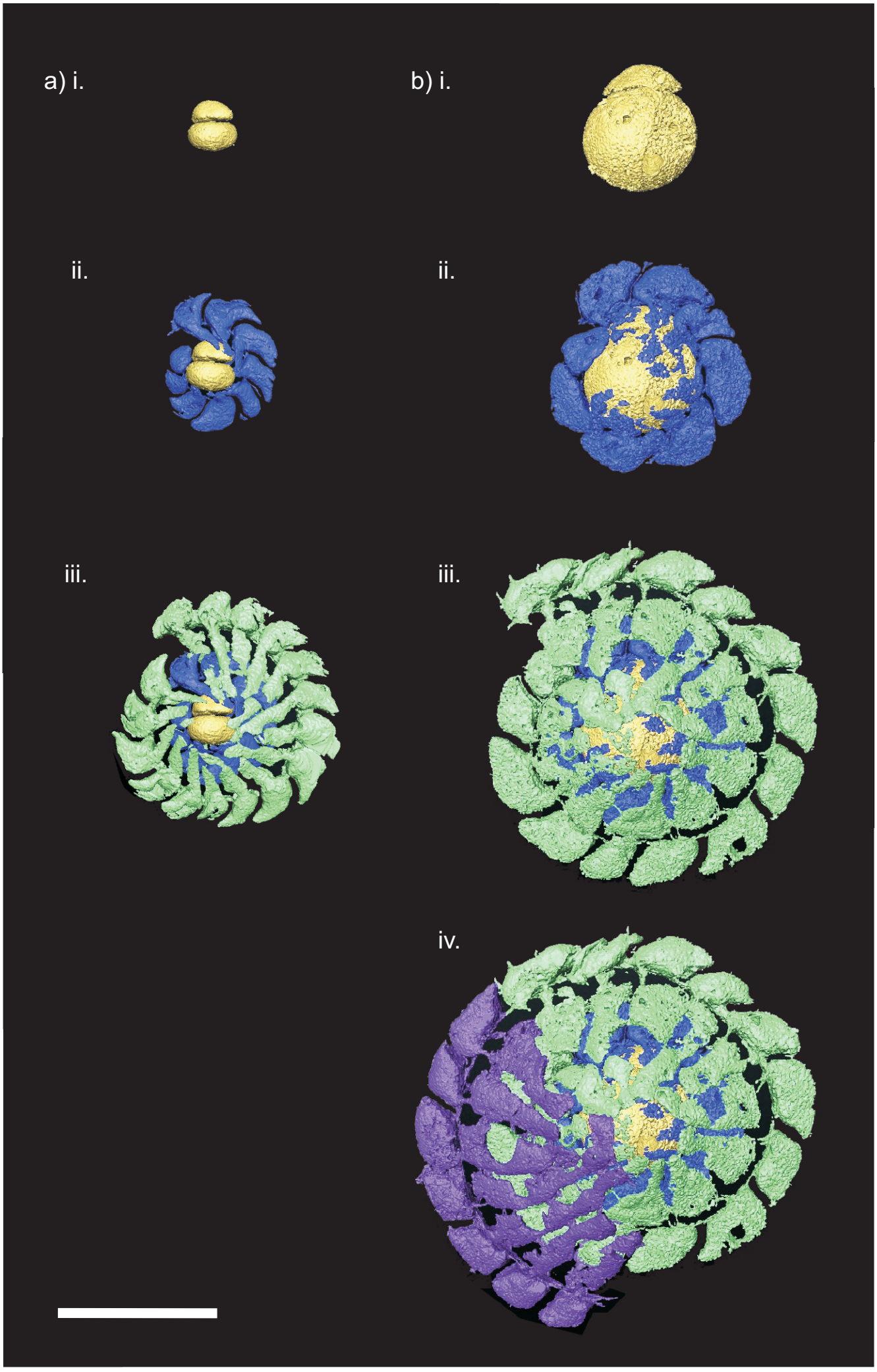

W3
W2
W1
WD
P1
P2
1
2
3
4
5
6
7
8
9
10


Time (Ma)
Stage
Planktonic foram zones Berggren et al. 1995
Planktonic foram zones Wade et al. 2011
TDP core stratigraphic position
38
39
40
41
42
43
44
45
46
47
48
49
50
Bartonian
Lutetian
Ypresian
P14
P13
P12
P10
P9
P8
P7
E13
E12
E11
E10
E9
E8
E7b
E7a
E6
4
18
2
TDP 4
TDP 18
TDP 2
Frequency
Proloculus size (μm)
0
2
4
6
8
10
100
200
300
400
500
600
700
800


a.
TDP4
b.
TDP18
c.
TDP2
d.
Mean
radius (µm)
Whorl number
WD
W1
W2
W3
0
200
400
600
800
1000
1200
1400
1600
N. ptukhiani
TDP 4
TDP 18
TDP 2


a.
b.
c.
d.
e.
f.
g.
h.
i.
j.
k.
l.


a.
b.
c.
d.
e.
f.
g.
h.
I.


a) i.
b) i.
ii.
ii.
iii.
iii.
iv.